

## Polyploidy and Aneuploidy in *Hypolepis*, and the Evolution of the Dennstaedtiales

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The fern genus *Hypolepis* is widespread in tropical and south temperate parts of the world. It has one center of distribution in southeastern Asia and Australasia (with a few species spreading as far as west Africa, Korea, the eastern Pacific and New Zealand) and another in the New World from the southernmost U.S.A. through Mexico and the Caribbean to Central and South America. Only one or two species of circumantarctic distribution are possibly common to both centers.

Morphologically the genus is fairly well defined, but the limits of individual species are much less obvious. Copeland (1947, p. 57) suggested that about 45 species should be recognized, although more recent investigations indicate that this is probably an underestimate. Particular problems arise in widely distributed, polymorphic taxa. These difficulties are compounded by the widespread and persistent misapplication of well known names such as *H. punctata* (Thunb.) Mett. and *H. tenuifolia* (Forst. f.) Bernh. and because many critical taxonomic features, notably the lamina and rachis hairs, are often poorly preserved or lost from old specimens, including many type collections.

The present paper is concerned with some of the wider implications resulting from a recent study of *Hypolepis* in Australia and New Zealand (Brownsey & Chinnock, in prep.). Although some of the ideas expressed here are speculative, they are put forward now in the hope of stimulating further research, particularly cytological investigation, into critical members of this group of ferns.

### MORPHOLOGY

*Hypolepis* includes species which have the following combination of characters: rhizomes long-creeping; fronds bipinnate or more compound, often large, free-veined; hairs, glandular or bristly, on some part of the lamina, rachis, stipe or rhizome; scales absent; sorus  $\pm$  round, ranging from terminal on a vein at the lamina margin, protected by a reflexed indusial flap or modified portion of the lamina, to submarginal, not quite terminating the vein, and totally unprotected; spores monolete.

These characters distinguish *Hypolepis* from allied genera, notably *Paesia*, *Pteridium*, and *Dennstaedtia*. In *Paesia*, the sori are continuous along the margins of the ultimate pinnules, borne on a marginal connecting vein, and protected both by the reflexed edge of the pinnule and by a distinct inner indusium. *Pteridium* is similar to *Paesia*, except that the inner indusium is less well developed and the spores are trilete. In *Dennstaedtia*, the spores are also trilete, but the marginal sorus is protected by a cup-shaped or slightly bivalvate indusium formed by the fusion of inner and outer indusia.

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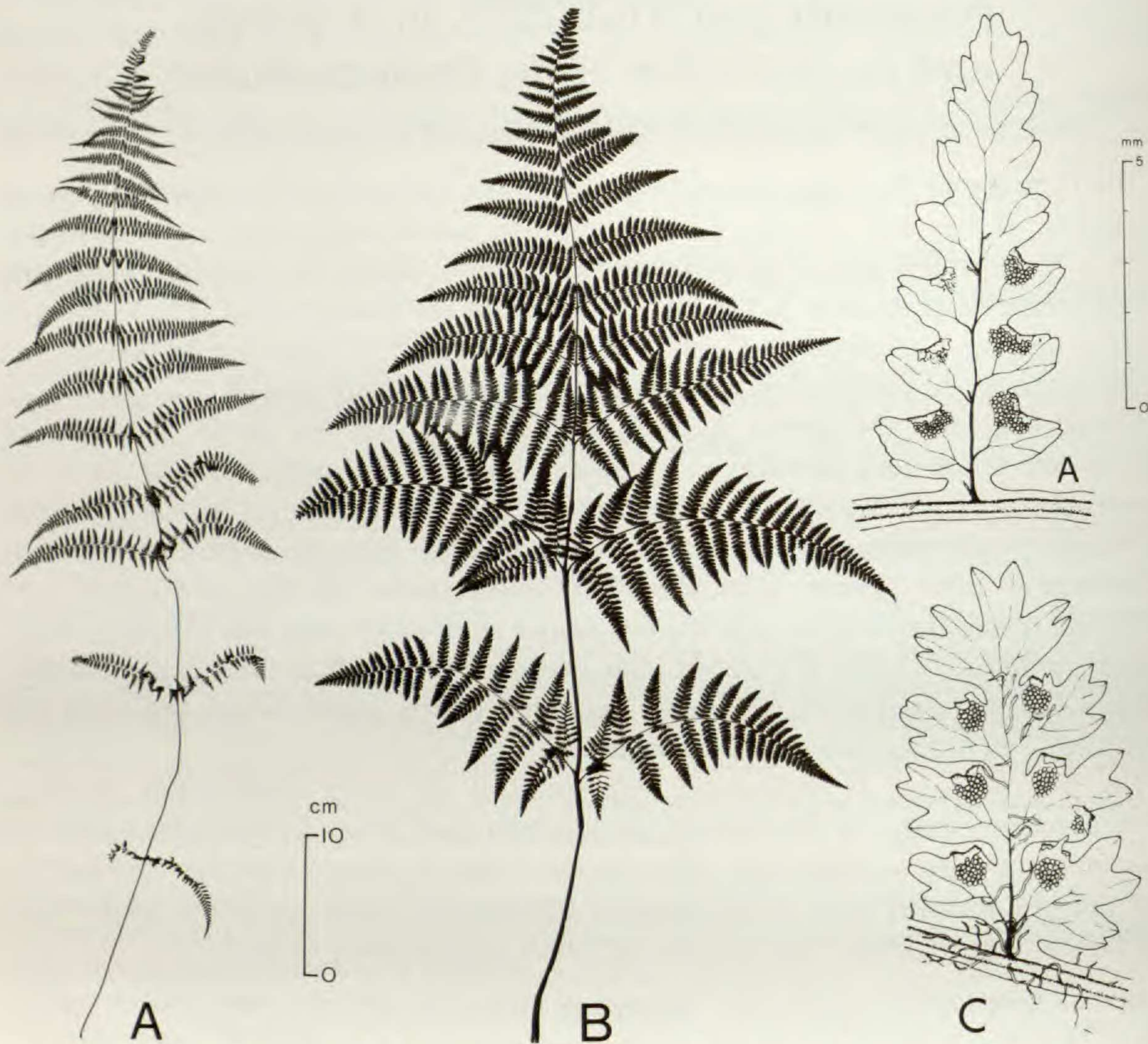


FIG. 1. Frond silhouettes and drawings of pinnules of *Hypolepis distans* (A) compared with *H. tenuifolia* sensu Allan (1961) (B) and *H. millefolium* Hook. (C).

Some species have been thought to transcend these generic boundaries. Mickel (1973) noted that an inner indusium was present in *Hypolepis bivalvis* v.A.v.R., but this taxon is better treated as *Paesia elmeri* Copel. (Holttum, 1958). More significantly, Bower (1928, fig. 587) reported the occasional presence of a vestigial inner indusium in *H. repens* (L.) Presl which he suggested linked *Hypolepis* with the Dennstaedtioid ferns, but this observation requires further investigation.

Many *Hypolepis* species are rather similar and must be distinguished by combinations of a few vegetative characters. In some cases, a well developed indusial flap is characteristic, but mostly their sori are unprotected. The hairs on the underside of the lamina are a key distinguishing character, varying in length, color, position, and glandularity. Also important are the degree of pinna dissection and the stipe and rachis color.

In Australia and New Zealand, *H. distans* Hook. stands out as being markedly different from the other ten or eleven species. The laminae are oblong-lanceolate and somewhat coriaceous, rather than characteristically deltoid and membranaceous;

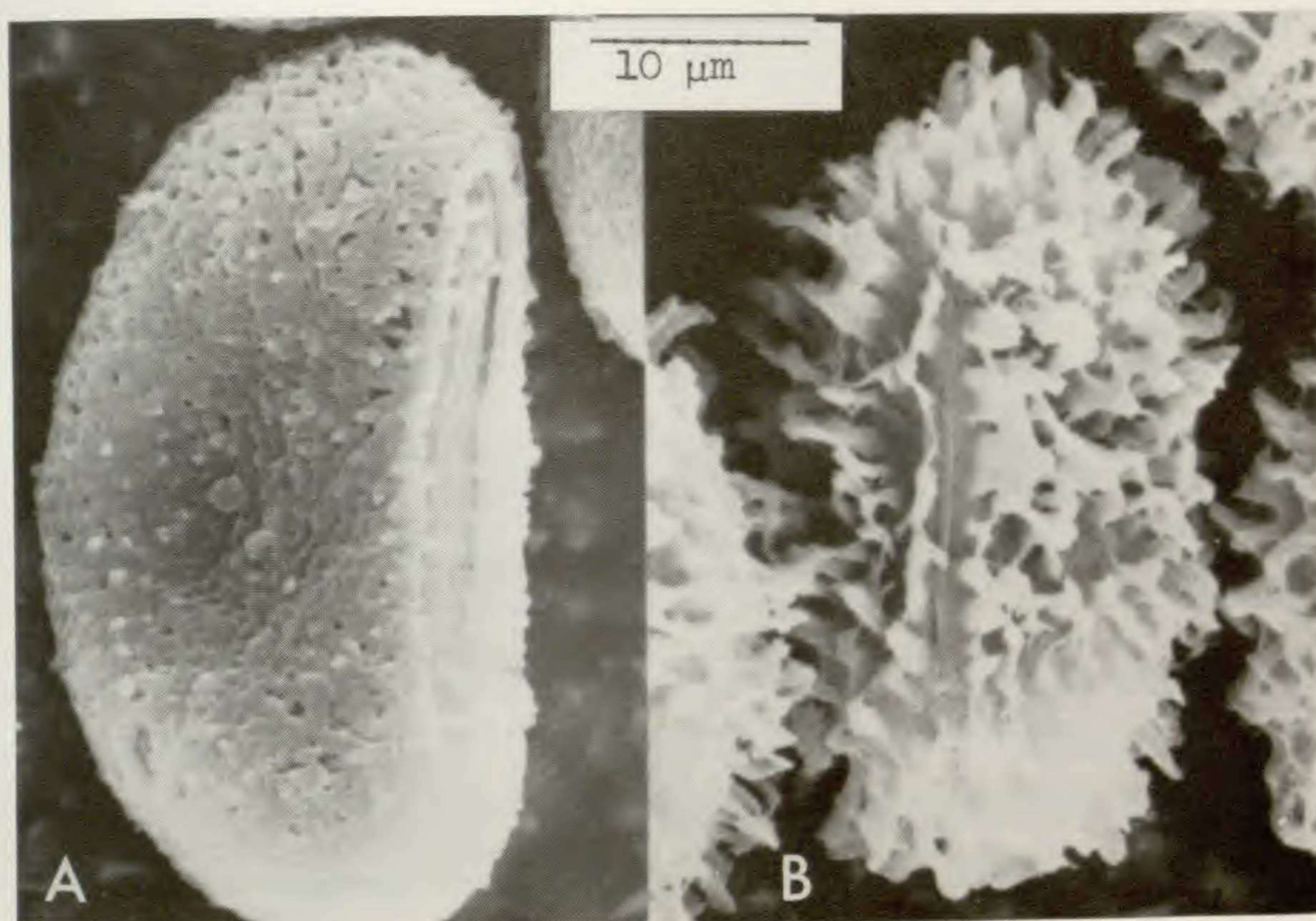


FIG. 2. Scanning electron micrographs of spores of *Hypolepis distans* (A) with a rather smooth perispore, and *H. rufobarbata* (Col.) Wakef. (B) with a perispore bearing numerous flattened projections.

the lower pinnae arise at  $90^\circ$  to the rachis (Fig. 1A), not at the usual acute angle (Fig. 1B); the stipes are very thin and highly polished, rather than generally thicker and hispid; and there are very few hairs anywhere on fronds of *H. distans*, which is unusual for *Hypolepis*. Most importantly, the veins of the ultimate pinnules end in emarginations (Fig. 1A) rather than in lobes (Fig. 1C). Finally, the spores of *H. distans* are very distinct, being dark brown and lacking any marked projections, in contrast to the spores of other species, which are pale and bear quite long, flattened projections (Fig. 2).

Species rather similar to *H. distans* are found in the New World, notably *H. nigrescens* Hook., which ranges from southern Mexico through Central America and the Caribbean to Colombia and Brazil, and the doubtfully distinct *H. hispaniolica* Maxon from the Dominican Republic and Haiti. *Hypolepis nigrescens* resembles *H. distans* in having coriaceous fronds, relatively few hairs on the lamina, pinnae arising at  $90^\circ$  to the rachis, veins ending in emarginations, and dark spores. On the other hand, it has rather thick stipes, which are pubescent and armed with sharp prickles, and spores which bear very fine spines. In these characters, *H. nigrescens* more closely resembles a distinctive group of *Hypolepis* species from southeast Asia represented by *H. brooksiae* v.A.v.R. and *H. papuana* Bailey. Like *H. nigrescens*, these species have a scrambling habit and periodic dormancy of the rachis (Holtum, 1958). Furthermore, their veins have a slight tendency to end in emarginations, but this is by no means so pronounced as in either *H. distans* or *H. nigrescens*. To what extent these three elements are related is not entirely clear from morphology alone.

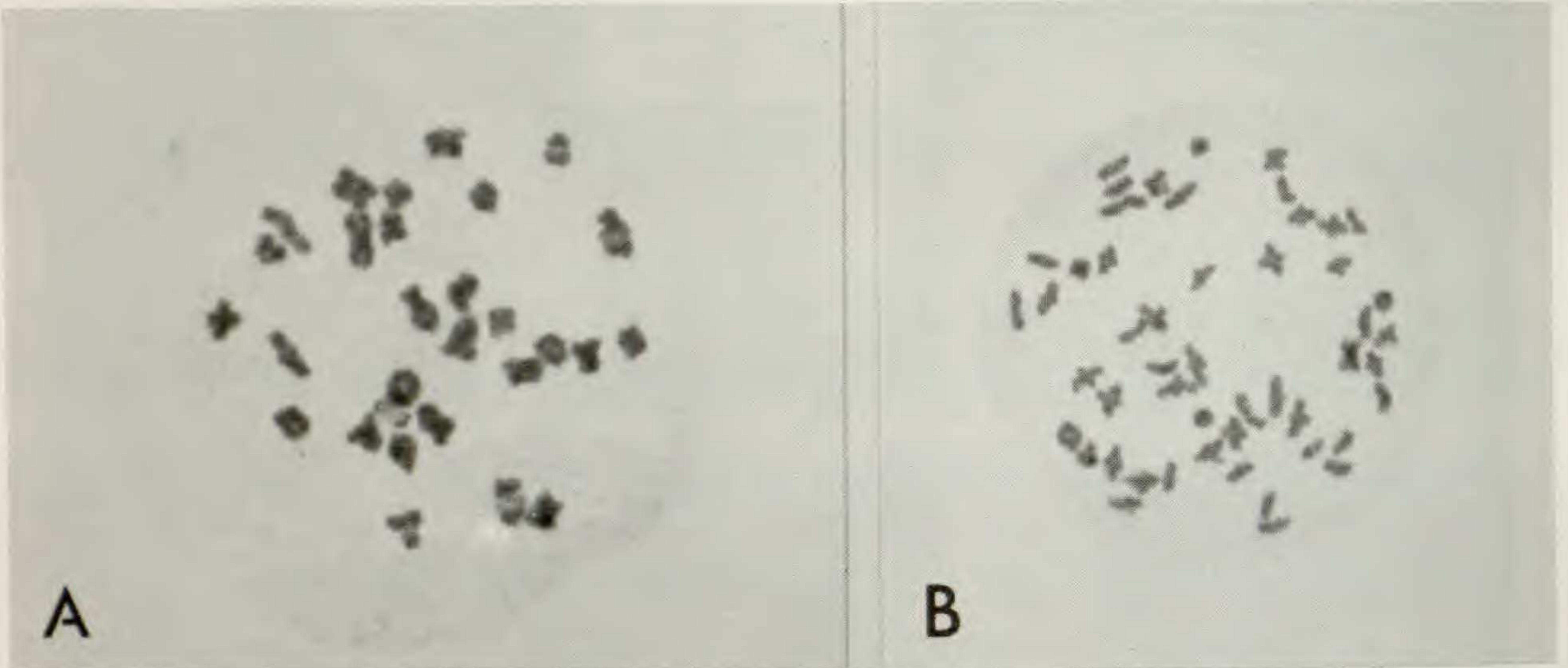


FIG. 3. Meiotic chromosome preparations ( $\times 1000$ ) from *Hypolepis distans* (A) Lake Kopureherehere, Levin, New Zealand, showing 28 bivalents, and *H. rufobarbata* (B) Kaituna Spur, Banks Peninsula, New Zealand, showing 52 bivalents. Voucher specimens in WELT.

#### HYBRIDIZATION AND CYTOLOGY

Evidence is accumulating that species of *Hypolepis*, like those of *Asplenium*, *Dryopteris* and *Polystichum*, have a considerable capacity for hybridization. There is good cytological evidence for this at different levels of ploidy among New World species of the genus and also in isolated records from Australia and Japan (*Table 1*). In New Zealand, hybridization in *Hypolepis* has long been suspected (Carse, 1929; Cockayne & Allan, 1934), and my own morphological and cytological investigations confirm this. Hybrids are recognizable by their intermediate morphology, shrivelled spores, and by the irregular pairing of their chromosomes at meiosis. Five of the six species of *Hypolepis* occurring on the main islands of New Zealand whose distributions overlap have been found to hybridize. Only *H. distans* does not appear to hybridize, which suggests, in common with the morphological and cytological evidence, that it is fundamentally distinct from the other native species.

My own unpublished results together with those of Brownlie (1954, 1957, 1958, 1961) indicate that of the six New Zealand species of *Hypolepis* other than *H. distans*, four have  $n=52$  (*Fig. 3B*) and two  $n=104$ . By contrast, plants from four populations of *H. distans* have  $n=28$  (*Fig. 3A*). Furthermore it is noteworthy that the chromosomes of *H. distans* are markedly larger than those of other New Zealand species (cf. *Figs. 3A* and *3B*).

Previously published cytological reports relating to species other than those in New Zealand are summarized in *Table 1*. All identifications are those of the original authors. Reports showing irregular meiotic pairing have been segregated as putative hybrids.

TABLE 1. CHROMOSOME COUNTS FOR SPECIES OF *HYPOLEPIS* FROM AREAS OTHER THAN NEW ZEALAND

Species	Origin	<i>n</i>	<i>2n</i>	Reference
OLD WORLD				
<i>H. punctata</i>	Japan	c. 104	-	Kurita, 1962
	Japan	98	-	Kurita, 1967, 1972
	Japan, Obarano	c. 92	-	Mitui, 1968
	Japan, Saitama Pref.	98	-	Mitui, 1975
	Japan, Niigata Pref.	98	-	Mitui, 1976
	Taiwan	52	-	Tsai, 1973
	Himalayas, Darjeeling	c. 102	-	Mehra & Khanna, 1959
	Himalayas, Mussoorie	104	-	Mehra & Verma, 1960
	Nepal, Kathmandu Valley	104	-	Roy et al., 1971
	Ceylon, Hakgala	51-53	-	Manton & Sledge, 1954
	Malaya, Taiping Hills	c. 100	-	Manton & Sledge, 1954
	Malaya, Taiping Hills	c. 104	-	Manton in Holttum, 1954
	Malaya, Fraser Hills	c. 104	-	Manton in Holttum, 1954
	<i>H. tenuifolia</i>	Samoa	-	104
<i>H. villos-viscidum</i>	Gough Island	c. 100	-	Manton & Vida, 1968
<i>H. sp.</i>	Australia	98	-	Kurita, 1972
<i>Hybrids</i>				
—	Australia	-	c. 150	Manton & Sledge, 1954
" <i>H. punctata</i> × <i>alte-gracillima</i> "	Japan	meiosis irregular	c. 200	II + I Kurita, 1967, 1972
NEW WORLD				
<i>H. repens</i>	U.S.A., Florida	104	-	Wagner & Chen in Löve & Solbrig, 1964
	Costa Rica, Platanillo	52	-	Smith & Mickel, 1977
	Puerto Rico, El Verde	39	-	Sorsa in Fabbri, 1965
<i>H. viscosa</i>	Mexico, Oaxaca	52	-	Smith & Mickel, 1977
<i>H. nigrescens</i>	Mexico, Oaxaca	29	-	Mickel et al., 1966
	Jamaica, Caledonia Peak	29	-	Walker, 1966
	Jamaica, Hardwar Gap	29	-	Walker, 1966
<i>Hybrids</i>				
" <i>H. bogotensis</i> "	Mexico, Chiapas	50II + 54 I	-	Smith & Mickel, 1977
" <i>H. aff. repens</i> "	Costa Rica, Platanillo	49II + 50 I	-	Smith & Mickel, 1977
" <i>H. aff. viscosa</i> "	Costa Rica, Cerro de la Muerte	52II + 52 I	-	Smith & Mickel, 1977

The majority of *Hypolepis* species so far investigated have chromosome complements of either  $n=52$  or 104. The various reported numbers for collections identified as *H. punctata* and *H. repens* strongly suggest that these taxa are ill-defined. My own morphological investigations suggest that counts for "*H. punctata*" may belong to as many as four different species from Japan and northern India, Taiwan, Ceylon, and Malaya, although without access to voucher material this cannot be verified. In the New World, there is clear evidence of polyploidy in *H. repens*, and it is also likely in the *H. bogotensis/viscosa* complex (Table 1), although

actual counts of  $n=104$  have yet to be demonstrated. Similarly, in Australia, the count from the hybrid plant with  $2n=c. 150$  strongly suggests the presence of parental species with  $n=52$  and  $104$ .

Of the anomalous numbers, the most improbable is  $n=39$  for *H. repens* from Puerto Rico which must be compared with  $n=104$  for the same species in Florida and  $n=52$  from Costa Rica. Such divergent numbers within a single species complex are hard to accept, notwithstanding their arithmetical relationship based on 13 and the undoubted fact that *H. repens* in Central and South America is an ill-defined aggregate (Stolze, 1981, p. 280).

Another curious number,  $n=98$  in Japanese plants of *H. punctata*, must be taken more seriously since it has been consistently reported from several populations and illustrated at least three times (Kurita, 1967, 1972; Mitui, 1975, 1976). Presumably it has arisen by aneuploidy, either by direct reduction from a parental species with  $n=104$ , or, earlier in its evolutionary history, from one with  $n=52$  (i.e. 52 to 49 to 98). The cells illustrated by Kurita (1972, fig. 11) and Mitui (1976, fig. 5) show some disparity in the size of individual bivalents consistent with the idea of reduction in chromosome number by fusion. Further investigation is required to ascertain the geographical distribution of this cytotype and the extent to which the loss of chromosomes is reflected in its external morphology. From a nomenclatural point of view, it is significant that the type of *H. punctata* is from Japan.

The report of  $n=29$  in *H. nigrescens* cannot be seriously doubted, having been independently reported by Mickel et al. (1966) from Mexico and by Walker (1966) from two populations in Jamaica. Furthermore, the number can now be very satisfactorily related to the discovery of  $n=28$  in *H. distans* from New Zealand. However, what is not known is whether there is a direct relationship between these two species, or whether they represent fragments of quite different aneuploid lines. While the morphological and cytological evidence confirms that *H. distans* and *H. nigrescens* (and probably also the *H. brooksiae/papuana* aggregate) are significantly different from most other members of the genus, it does not yet resolve the relationship between the three elements.

In summary, these cytological observations point to a base number of  $x=26$  in *Hypolepis*, despite the fact that such a number has yet to be recorded for the genus. There is a well established polyploid line of evolution represented by the numbers  $n=104$  and  $52$  that is almost certainly derived from  $n=26$ , and there is the more recently demonstrated evidence of aneuploidy, with  $n=29$  in *H. nigrescens* and  $n=28$  in *H. distans*, that can also be related to  $n=26$  (Fig. 4). The former existence of  $n=26$  in *Hypolepis* is indirectly supported by cytological observations from *Paesia*, where the numbers  $n=26$  and  $104$  have been reported, and from *Pteridium*, where  $n=26$ ,  $52$ , and  $104$  are all known (for original references see Löve, Löve & Pichi Sermolli, 1977, p.189). Although a base as low as 13 is theoretically possible, it seems highly unlikely unless the count of  $n=39$  from Puerto Rican plants of *H. repens* can be confirmed. On the other hand there is a strong possibility that the primitive number in the genus may actually be 29, from which species having  $n=26$  were derived by aneuploidy, ultimately giving rise to a successful polyploid line of evolution radiating at the tetraploid and octoploid levels.

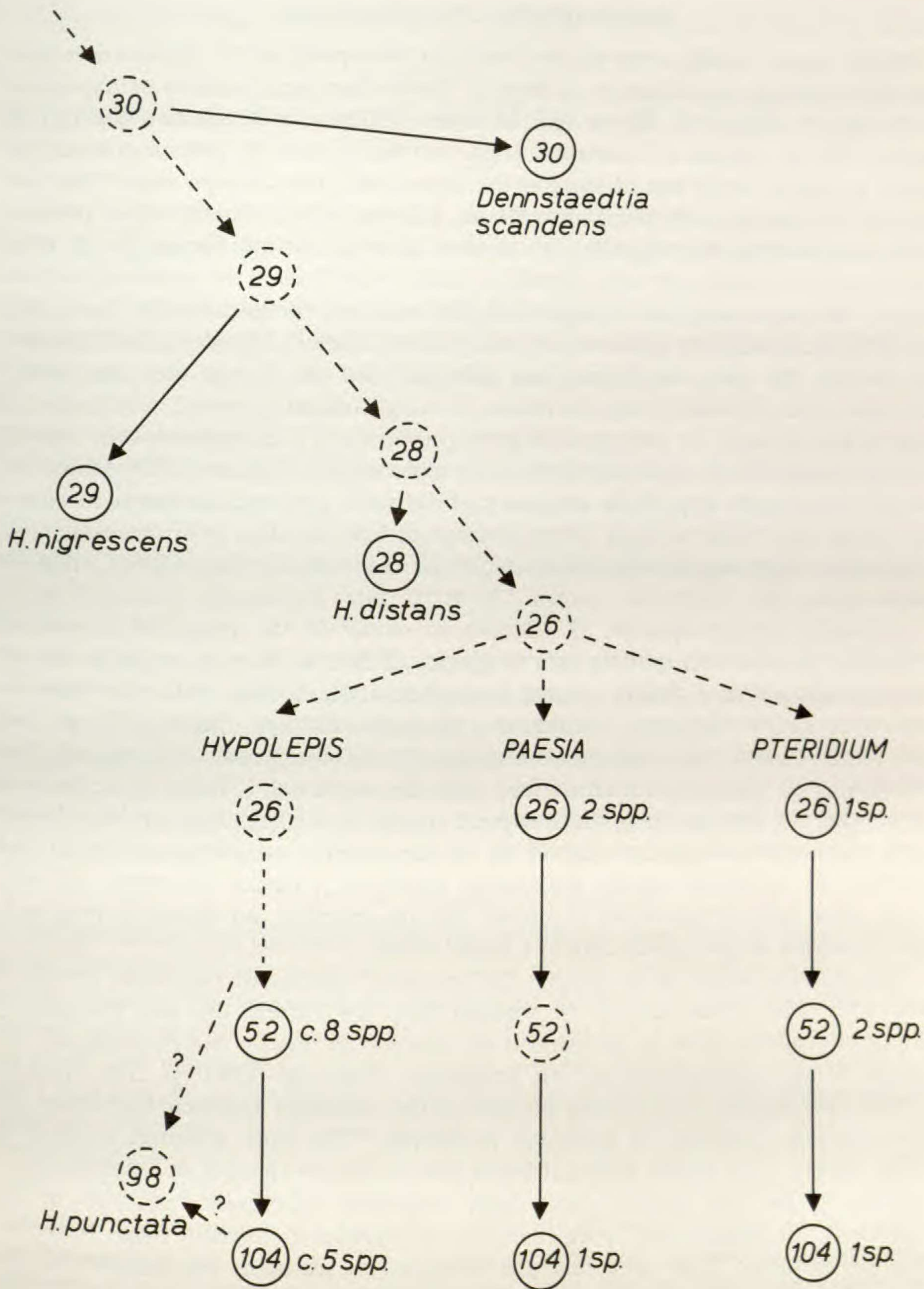


FIG. 4. Phyletic scheme deriving the Hypolepidaceae from the Dennstaedtiaceae. Solid lines and numbers in unbroken circles indicate probable lines of evolution and established chromosome numbers. Broken lines and numbers in broken circles indicate possible lines of evolution and doubtful or postulated cytotypes.

### PHYLOGENETIC CONSIDERATIONS

Mickel (pers. comm.) has pointed out that the spores of *H. distans* are more similar in their perispore pattern to those of *Paesia* than to any species of *Hypolepis*, including *H. nigrescens*. He recognized some similarity in frond form between *H. distans* and the species of *Paesia* and suggested that it could be part of an aneuploid series in *Paesia* which has resulted in the loss of the characteristic inner indusium. Despite the similarity of its spores to *Paesia*, I do not believe that this alone provides sufficient evidence for regarding *H. distans* as a species of *Paesia*. In all other characters it is consistent with *Hypolepis* rather than *Paesia*: the inner indusium is absent; the sorus terminates a single vein; the veins are conspicuous (in *Paesia* they are difficult to see); the veins end in emarginations (rare in *Hypolepis*, but unknown in *Paesia*); the hairs are scarce and non-glandular (in *Paesia* they are usually abundant and glandular); and the rachis is straight, bearing pinnae which arise at right angles in more or less opposite pairs (in *Paesia* it is characteristically zig-zag bearing pinnae which arise alternately at an acute angle). Holttum (1958) related the shape of the rachis to periodic dormancy of the apex, pointing out that in *P. elmeri* the rachis rests while a single pinna develops in turn, but that in *H. brooksiae* and other genera showing periodic dormancy, a pair of pinnae develop together while the rachis rests.

Although, in my opinion, *H. distans* is closer to the polyploid species of *Hypolepis* (with  $n=52$  or  $104$ ) than to species of *Paesia*, there is no doubt that all three groups are very closely related. Nevertheless, *H. distans*, with or without *H. nigrescens* and *H. brooksiae*, constitutes a distinctive element. Smith (1981, p. 136) has already noted the cytological heterogeneity of the genus and suggests that "*Hypolepis* as presently circumscribed may be unnatural." There is certainly a strong case for distinguishing the aneuploid species from the polyploid, but whether such taxonomic recognition should be at the generic or subgeneric level, and whether the aneuploid species themselves constitute a natural grouping, are very much more difficult questions to answer. For the moment, no change is proposed, and *Hypolepis* is interpreted here in a broad sense.

The question arises as to whether the aneuploid species of *Hypolepis* provide a link with other allied genera, or whether they are merely the end products of divergent evolution from an ancestral stock with  $n=26$ . *Paesia* and *Dennstaedtia* are central to any consideration of this possibility. Copeland (1947, p. 57), Holttum (1949), and Mickel (1973) have pointed to the similarity between *Hypolepis* and *Dennstaedtia*, Copeland in particular remarking "The more primitive element in [*Hypolepis*] . . . is hardly distinguishable from a similar element in *Dennstaedtia*." Species of the two genera share many vegetative characters, although in my experience the indusial and spore characters will always distinguish them. Nevertheless, the presence of an aneuploid line in *Hypolepis* including the numbers 28 and 29 is of considerable interest since it ties in remarkably with the numbers 30–34, 46, and 47 so far known in *Dennstaedtia* (Lovis 1977, p. 275; Löve et al. 1977, p. 184). These numbers have already been cited by Lovis (1977, p. 303) in postulating that the evolution of the Dennstaedtiaceae (i.e., Pichi Sermolli's Dennstaedtiales) is the result of a long series of aneuploid reductions from a base in the Cyatheaceae.



It may be more than mere coincidence, therefore, that *Hypolepis brooksiae* bears a quite extraordinary morphological similarity to *Dennstaedtia scandens* (Blume) Moore. In the field both are scrambling, thicket-formers with periodic dormancy of the rachis (Holttum, 1958); in the herbarium they can be distinguished only by a very careful scrutiny of the indusium or by the spores. It is highly significant that Tsai (1973) has reported the chromosome number of *D. scandens* in Taiwan to be  $n=30$ . Unfortunately, the chromosome number of *H. brooksiae* is not yet known, but if, as its morphological similarity to *H. distans* and *H. nigrescens* suggests, the number proves to be in the high 20's, this would constitute good evidence of an evolutionary link between *Dennstaedtia* and *Hypolepis*.

Some features of *H. distans*, notably the pronounced emarginations, the thin, highly polished stipes, and the virtually glabrous fronds, are not typical of *Dennstaedtia*. One possible answer to this paradox may be that *H. nigrescens*, *H. distans*, and perhaps *H. brooksiae*, represent remnants of unstable karyotype combinations thrown up in the course of a series of aneuploid reductions from a source in *Dennstaedtia* extending back to at least  $x=34$  and possibly as far as  $x=47$ . An unbroken series of base numbers from 34 in *Dennstaedtia punctilobula*, through 33 or 32 in *D. scabra*, 31 in *D. wilfordii*, 30 in *D. hirsuta* and *D. scandens*, 29 in *Hypolepis nigrescens*, and 28 in *H. distans*, ultimately giving rise to a felicitous combination of 26 chromosomes in *Paesia*, *Pteridium*, and the polyploid species of *Hypolepis*, is an entirely plausible evolutionary pathway (Fig. 4). The very fact that many of the same characters appear in different combinations in the four genera reinforces the belief that these genera do share a common origin. For example, *Dennstaedtia*, *Paesia* and *Pteridium* have an inner indusium, but *Hypolepis* does not; *Dennstaedtia* and *Hypolepis* have sori terminating a single vein, whereas *Paesia* and *Pteridium* have sori linking several veins; *Dennstaedtia* and *Pteridium* have trilete spores, whereas *Hypolepis* and *Paesia* have monolete spores.

#### LIMITS OF THE HYPOLEPIDACEAE

The possibility that members of the Hypolepidaceae were derived from a source in the Dennstaedtiaceae necessitates a more careful consideration of the genera which constitute the former family. There is no doubt in my mind that *Hypolepis*, *Paesia*, and *Pteridium* form a natural group of genera with a common ancestry based on  $x=26$  and that they are related to—and possibly derived from—*Dennstaedtia*, but I find it much more difficult to ally them with some of the other genera which have been referred to the Hypolepidaceae.

The family was first circumscribed and its relationships outlined by Pichi Sermolli (1970, 1977, p. 431). He included in it *Hypolepis*, *Paesia*, *Pteridium*, *Histiopteris*, *Lonchitis*, and *Blotiella*. To these (as subfamily Hypolepidoideae of the Dennstaedtiaceae) Lovis (1977, p. 276) added *Monachosorum*, *Taenitis*, and *Idiopteris*, although most workers would now probably agree that the latter two genera are better placed with the Gymnogrammeoid and Pteridoid ferns, respectively.

The true affinities of *Monachosorum* have never been satisfactorily established, but it fits no better in the Hypolepidaceae than in any of the other families to which it has been assigned (Christensen, 1938; Holttum, 1947; Copeland, 1947, p. 51;

Mickel, 1973). Lovis's main reason for putting it with the Hypolepidaceae was the belief that  $n=56$  in *M. maximowiczii* (Bak.) Hayata might have been derived from  $x=28$ , which relates to known numbers in *Hypolepis*.

*Lonchitis* and *Blotiella* have also been regarded as somewhat discordant elements in the Hypolepidaceae, both by Mickel (1973) and even by Pichi Sermolli (1977, p. 432). Their chromosome numbers ( $n=50$  and  $38$ ) do not fit at all comfortably.

There remains the genus *Histiopteris*, which Mickel (1973) and Pichi Sermolli (1977, p. 432) found no difficulty in allying to *Hypolepis*, *Paesia*, and *Pteridium*. However, Copeland (1947, p. 60) considered it related to *Pteris*, and Holttum (1973) included it in his list of genera whose relationships need "fresh examination." My own experience of *Histiopteris* in New Zealand suggests that it is not closely allied to other members of the Hypolepidaceae. The presence of scales on the rhizome, glaucous and virtually glabrous fronds, anastomosing veins, and sessile pinnae are all characters alien to *Hypolepis*, *Paesia*, and *Pteridium*. Most importantly, the known chromosome numbers of  $n=48$  and  $96$  (Löve et al. 1977, p. 191) cannot easily be related to a base of  $26$  in the other genera.

Assuming that *Monachosorum*, *Lonchitis*, *Blotiella*, and *Histiopteris*, if not members of the Hypolepidaceae, are at least Dennstaedtialean, room must obviously be found for them elsewhere. Crabbe et al. (1975, p. 155) have already proposed for *Monachosorum* a monogeneric subfamily, Monachosoroideae, within their Dennstaedtiaceae (equivalent to Pichi Sermolli's Dennstaedtiales), and a solution of this nature may be necessary for the other genera.

#### EVOLUTION OF THE DENNSTAEDTIALES SENSU PICHI SERMOLLI

Looking beyond the Hypolepidaceae, Wagner (1980) has recently proposed that the neotropical genus *Loxomopsis* might have an "affinity to either the dennstaedtioid or lindsaeoid ferns" on account of its chromosome number of  $n=46$ . This contrasts with  $n=50$  reported for *Loxosoma* (Brownsey, 1975), a genus previously considered very close to *Loxomopsis* but whose relation to other genera has always been very uncertain. Investigation of its gametophytes by Stokey and Atkinson (1956) and of its stomata by van Cotthem (1970, 1973) suggested an affinity between Loxsomaceae and Cyatheaceae, but the cytological evidence indicates that any such relationship must be fairly remote. However, Lovis's (1977, p. 303) suggestion that the Dennstaedtiaceae (i.e., Pichi Sermolli's Dennstaedtiales) originated by a long series of aneuploid reductions from a source in the Cyatheaceae provides a means of reconciling these differences. If *Loxosoma* and *Loxomopsis* are admitted to be Dennstaedtialean ferns, as at least some of their morphological characters and certainly their chromosome numbers suggest, then the distant affinity with the Cyatheaceae, hinted at by the gametophyte and stomatal characters, lends some support to Lovis's hypothesis.

It may be that the troublesome *Monachosorum* also belongs on the evolutionary line from the Cyatheaceae to the Dennstaedtiales. Its position here could help to reconcile the views of Copeland (1947), Crabbe et al. (1975), and Pichi Sermolli (1977, p. 430), who allied it with the Dennstaedtiaceae, with those of Christensen (1938), who allied it with the Thelypteridaceae; in both Holttum's (1973) and

Lovis's (1977, fig. 3) scheme, the latter family is itself an offshoot of the Cyatheaceae. Certainly the chromosome number of *Monachosorum* ( $n=56$ ) fits better here than in the Hypolepidaceae. Moreover, the numbers 46, 50, and 56 now established in *Loxsomopsis*, *Loxsoma*, and *Monachosorum* go some way to bridging the gap between the highest confirmed number of  $n=48$  in the Dennstaedtiales (Lovis, 1977, p. 304) and the range of 56–69 (excepting 95 or 96 in *Metaxya*) in the Cyatheaceae sensu Lovis (1977, p. 273).

This leaves an awkward group of genera, *Blotiella* ( $n=38$ ), *Histiopteris* ( $n=48$ ), and *Lonchitis* ( $n=50$ ), whose affinities are far from clear. *Blotiella* and *Histiopteris* have much in common morphologically, but cytologically the latter genus is closer to *Lonchitis*. Tryon (1962) suggests that *Blotiella* is related to *Hypolepis*, but that *Lonchitis* is closer to *Pteris*. *Histiopteris* has also been allied with both the Dennstaedtialean and Pteridoid ferns, but its cytology fits comfortably into neither group; the Pteridoid ferns are clearly based on  $x=29$  or  $30$ , albeit with an aberration of  $n=27$  in *Idiopteris*, while the known range in Dennstaedtialean ferns (26–c. 50) would require *Histiopteris* to be placed at the higher end of the cytological spectrum where its morphology is even more out of place than at the lower end with the Hypolepidaceae. The affinities of these three genera need to be more thoroughly investigated; meanwhile, I regard their placement as uncertain.

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